with stronger non-photochemical energy dissipation as the use of absorbed light for photochemistry becomes restricted (Abdullaev et al., 2024). Consistent with this, droughted wheat often exhibits lower Fv/Fm and Fv/F0, linking reduced gas exchange with reduced photochemical efficiency of PSII. These responses indicate that the photosynthetic apparatus is not only receiving less CO_2 because of stomatal closure, but is also redistributing excitation energy toward protective heat dissipation.

However, PSII damage is usually limited during mild drought and becomes pronounced mainly under severe dehydration, when protective mechanisms are no longer sufficient (Sommer et al., 2023). Under stronger stress, wheat shows increases in F0 and decreases in Fm, Fv/Fm, qP, and ETR, while OJIP-based indices such as RC/ABS, PIabs, and PItot also decline, revealing fewer active reaction centers and lower overall PSII performance. Mechanistically, drought reduces PSII electron transport and leaves a larger fraction of absorbed energy to be handled by alternative electron sinks and cyclic electron flow, which appear to contribute to photoprotection. Fluorescence traits therefore capture both injury and acclimation, making them useful indicators for distinguishing tolerant and sensitive wheat genotypes.

3.3 Photosynthetic pigments, carbon assimilation, and photosynthetic product accumulation

Drought commonly reduces photosynthetic pigment content in wheat leaves, including chlorophyll and carotenoids, and this loss contributes directly to lower light capture and weaker carbon assimilation. Reviews and experiments converge on the point that drought-induced chlorophyll decline is associated with chloroplast damage, thylakoid disruption, and reduced activity of Calvin-cycle components such as Rubisco, which together depress atmospheric carbon fixation. At the molecular level, drought also down-regulates many wheat genes linked to PSI, PSII, light-harvesting complexes, cytochrome b6f, and ATP synthase, providing a transcriptional basis for declining pigment function and photochemical capacity (Karami et al., 2025). Because tolerant cultivars usually retain chlorophyll more effectively, pigment stability is often treated as a practical marker of drought resilience.

The reduction in leaf carbon assimilation under drought also changes downstream carbohydrate metabolism and assimilate accumulation. As photosynthesis falls, starch accumulation is often reduced, while soluble sugars and sucrose-related metabolism become more dynamic and can increase as part of osmotic adjustment or stress reallocation (Nyaupane et al., 2024). In developing wheat grains, drought during early grain filling significantly increases soluble sugars and sucrose synthase activity, while sucrose and total starch can first decline and then rebound, indicating a temporal restructuring of carbon partitioning rather than a uniform shutdown. Experimental manipulation also shows that improving stress protection can preserve chlorophyll and moderate drought-induced shifts in sucrose and starch pools, reinforcing the close coupling between leaf photosynthetic performance and whole-plant carbon economy.

4 Drought-Induced Oxidative Stress and Reactive Oxygen Species Metabolism

4.1 Production and accumulation of reactive oxygen species

Drought stress triggers a rapid increase in reactive oxygen species (ROS) production in wheat leaves because stomatal closure restricts CO_2 fixation, causing absorbed light energy and reducing power to exceed the utilization capacity of the Calvin cycle. This excess excitation energy drives electron leakage to molecular oxygen, primarily generating superoxide ($O_2{\bullet}^-$) and hydrogen peroxide (H_2O_2) in chloroplasts, peroxisomes, and mitochondria. Under normal conditions, only a small fraction of electrons passing through the electron transport chain incompletely reduce oxygen, but drought shifts this balance toward uncontrolled ROS generation. The resulting overaccumulation of ROS disrupts cellular redox homeostasis and initiates oxidative cascades that damage biomolecules (Panda et al., 2024).

ROS accumulation in wheat is highly dependent on drought severity and duration. Under progressive drought, ROS levels remain stable during early stress phases but increase significantly once drought exceeds a critical threshold, indicating that the ROS generation rate eventually overwhelms the plant's scavenging capacity. Drought-sensitive wheat cultivars accumulate higher ROS levels than tolerant ones, reflecting greater photosynthetic inhibition and a higher potential for oxidative damage. Tolerant cultivars mitigate ROS accumulation through enhanced non-photochemical quenching and sustained antioxidant enzyme activity, which